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Body size, age, growth and alternative mating tactics in toads: satellite males are smaller but not younger than calling males

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Body size–age relationships may have important implications for the evolution and maintenance of alternative mating tactics, but these relationships remain largely unexplored in anuran amphibians (frogs and toads). In a single territorial anuran species, smaller noncalling 'satellite' males are younger than calling males. These results have led to the general assumption that such an age difference also holds for other anuran species with body size differences among behavioural phenotypes. However, individuals of many organisms show different developmental and/or growth trajectories that correspond to variation in adult morphology and behaviour. To test the generality of smaller satellite males being younger than larger calling males in anurans, we examined body size–age–behaviour relationships in Woodhouse's toads, *Bufo woodhousii*, and Great Plains toads, *B. cognatus*. Age estimates, based on skeletochronologic analysis of lines of arrested growth (LAGs) from phalanges, indicated that males sampled while adopting a noncalling satellite tactic were smaller, but not younger, than males sampled while adopting a calling tactic. Furthermore, examination of inter-LAG areas of bone deposition indicated that smaller satellite male *B. woodhousii* showed lower growth rates relative to calling males. A similar trend occurred for *B. cognatus*. We discuss our results in the context of developmental patterns associated with alternative mating tactics in other species and endocrine regulation of behavioural tactics in anurans.

Within a species, individuals often differ in their mating behaviour (reviewed by Rubenstein 1980; Gross 1986; Shuster & Wade 2003; West-Eberhard 2003). Such variation in behaviour can stem from energetic constraints associated with differences in body size (Halliday 1987, 1992; Tejedo 1992; Andersson 1994). For example, small males are generally less likely to sustain energetically demanding reproductive behaviours that may result in mating advantages for large males (Andersson 1994). In anuran amphibians (frogs and toads), the energetic cost of vocal production is typically high (Bucher et al. 1982; Pough et al. 1992; Prestwich 1994; Wells et al. 1995; Wells 2001), and male mating success is often positively correlated with calling persistence, vigour, chorus tenure and body size (i.e. Woodward 1982; Sullivan et al. 1995; Judge & Brooks 2001; Gerhardt & Huber 2002). The metabolic demands associated with vocal production may, in turn, lead to the expression of alternative noncalling mating

tactics (Lucas & Howard 1995; Lucas et al. 1996; McCauley et al. 2000; Emerson 2001; Leary et al. 2004).

Alternative 'satellite' mating tactics are common in anurans (Waltz 1982; Halliday & Tejedo 1995). Males practising a nonvocalizing satellite tactic typically reside in close proximity to calling conspecific males and attempt to intercept females attracted to the calling host(s) (reviewed by Halliday & Tejedo 1995). Individuals can alternate between calling and satellite tactics within and between bouts of chorus activity (Halliday & Tejedo 1995; Lucas & Howard 1995; Lucas et al. 1996), and small males are often more likely to adopt noncalling mating tactics than are large males (reviewed by Halliday & Tejedo 1995; Gerhardt & Huber 2002).

Because of the size difference between males practising alternative mating tactics, satellite behaviour in anurans is generally considered to be a conditional tactic (sensu Gross 1986) adopted by smaller, and presumably younger, competitively inferior males (reviewed by Halliday & Tejedo 1995; Gerhardt & Huber 2002). For example, Forester & Thompson (1998) assumed that satellite male American toads, *Bufo americanus*, were younger than calling individuals based on body size differences. Such

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presumed body size–age relationships may have implications relative to developmental constraints and the maintenance of alternative mating tactics (Brockmann 2001). For instance, constraints associated with life history characteristics (i.e. ontogenetic changes in body size) may maintain a subset of smaller, younger individuals within the population that typically adopt the alternative mating tactic. This relationship has been documented in bullfrogs, *Rana catesbeiana*, where males commonly engage in combat to defend territories from rival males, and larger males typically win contests over calling sites (Howard 1978, 1984).

Evidence suggests that the probability that an individual adopts a satellite tactic is mediated by the depletion of energy reserves during aggressive interactions, vocal production, or both (Robertson 1986a, b; Tejedo 1992; Halliday & Tejedo 1995; Leary et al. 2004). Hence, the common body size discrepancy between large callers and small satellite anurans may not necessarily reflect differences in tactic use by individuals of different ages, but rather that smaller individuals are subject to metabolic constraints that predispose them to less energetically demanding mating tactics. Although size-based estimates may, in some cases, accurately reflect age differences among callers and satellites, it is possible that callers and satellites show disparate developmental and/or growth trajectories that affect the adult phenotype and behaviour (reviewed by West-Eberhard 2003).

In a previous study on Woodhouse's toads, *Bufo woodhousii*, and Great Plains toads, *B. cognatus*, we found that individuals alternated between behavioural tactics and satellite males were significantly smaller than calling conspecifics (Leary et al. 2004; see also Sullivan 1983; Krupa 1989). In the present study, we further examined size–behaviour relationships in these species to determine whether smaller males practising the satellite tactic are younger than calling conspecifics or, alternatively, if morphological differences are the result of disparate growth trajectories among individuals of the same age.

METHODS

Animals and Behaviour

We examined body size–age relationships of satellite and calling male *B. woodhousii* and *B. cognatus* from choruses in central Oklahoma, U.S.A., that were studied in our previous investigation (Leary et al. 2004) and from southeast Arizona, U.S.A. In the present study, data were obtained from a total of 53 *B. woodhousii* ($N = 39$ callers, $N = 14$ satellites) from central Oklahoma (Cleveland County) and 26 *B. cognatus* (20 from central Oklahoma, Cleveland and Canadian counties: $N = 13$ callers, $N = 7$ satellites; 6 from Cochise County, Arizona: $N = 3$ callers, $N = 3$ satellites).

All data for *B. woodhousii* were obtained from the same population over three consecutive nights of chorus activity on 10, 11 and 12 April 2002. Data for *B. cognatus* from central Oklahoma were obtained from three populations during chorus activity on 13 April 2002, and 16 May and

10, 12 June 2003. All data were collected during periods of peak chorus activity for both species (typically around 2300–0100 hours). To avoid sampling the same individuals between years, individual *B. cognatus* from 2002 and 2003 were sampled from different populations. Data for *B. cognatus* from Arizona were obtained from a single chorus on 19 and 22 July 2003. Populations from Oklahoma and Arizona were closely monitored throughout the years of study. Data were obtained during the first, second, or third night of chorus activity for that population for any given year to avoid comparing data from individuals collected at different times of the year because differences in annual growth (i.e. total bone deposition) could alter age estimates and/or growth estimates.

Callers and satellites were classified during 10–25-min focal observations (see Leary et al. 2004). Noncalling males of these species attempt to intercept females approaching calling males and are not merely awaiting vacancy of calling sites (Sullivan 1982, 1983, 1989; Krupa 1989). Our observations corroborate previous reports in that it was common for noncalling males to amplex nearby males and/or incoming females in our observational time frame. Satellite males can be readily identified because they typically assume a low posture and remain in close proximity to calling males (Sullivan 1982, 1983, 1989; Krupa 1989).

Satellite behaviour for the two species differs in that satellite *B. woodhousii* characteristically patrol the periphery of the chorus and do not associate with a specific calling host male, whereas satellite *B. cognatus* typically associate with a single vocalizing male, often for prolonged periods (Sullivan 1982, 1983, 1989; Krupa 1989; Leary et al. 2004). In all cases, data were obtained from a satellite and nearby calling males. More samples were obtained from callers because callers were more abundant than satellites. Although an individual male can alternate between tactics in these species, the probability of observing a male practising a given tactic should be proportional to the amount of time the male spends displaying that tactic. Thus, comparing groups of males practising the two tactics should accurately reflect the distribution of males that are more likely to adopt either tactic.

Following focal observations, individuals were captured by hand and measured (to the nearest 1 mm) from the snout to end of the ischium and marked in sequence on the venter with a portable tattoo device (Tattoo-A-Pet, Inc., Fort Lauderdale, Florida, U.S.A.) for future identification. The third digit of the right rear foot was amputated at the joint immediately proximal to the penultimate phalange and placed in 10% buffered formalin. Immediately following amputation, the distal portion of the remaining digit was treated topically with Bactoderm antibiotic ointment (Mupirocin, SmithKline Beecham Pharmaceuticals, Philadelphia, Pennsylvania, U.S.A.) by a veterinarian (A.M.G.) and animals were released. Amputated digits showed no signs of infection or necrosis upon examination on subsequent recaptures both within and between years (A.M.G., personal observation). All procedures followed the guidelines for the use of amphibians in research outlined by the American Society of Ichthyologists and Herpetologists, the Herpetologists' League, and

the Society for the Study of Amphibians and Reptiles (http://www.asih.org/pubs/herpcoll.html). All procedures were approved by the University of Oklahoma Animal Care and Use Committee (R01-005).

Histology

We used skeletochronology to estimate age based largely on the procedures outlined by Redmer (2002). Briefly, toes were removed from buffered formalin and placed in a 1% trypsin solution for 3–5 h to remove surrounding soft tissue from the bone. The penultimate phalange was then decalcified in a 5% formalin–nitric acid solution for 48 h and subsequently neutralized in 5% sodium sulfate. Phalanges were run through a series of ethanol washes (1 h each in 30%, 50%, 70%, 90%, and then 5 h in 100%

ethanol) and placed in Citrisolv (Fisher Scientific, Pittsburgh, Pennsylvania) overnight. Phalanges were then embedded in paraffin and sectioned at 15 μm. Sections were run through a series of Citrisolv and ethanol washes, rinsed in water, stained with Erlich's haematoxylin, and counterstained with phloxine eosin.

Age was determined by counting lines of arrested growth (LAGs) from diaphyseal sections of phalanges (Fig. 1). These lines appear as dark-stained rings that correspond to periods of hibernation in anurans and have been shown to accurately estimate age in numerous amphibian species (Halliday & Verrell 1988; Hemelaar 1988; Flageole & LeClair 1992; Guarino et al. 2003). Age estimates were assessed independently by two observers with no prior knowledge of the behavioural phenotype being examined. Age estimates ascertained by the two scorers were identical for 69 of 79 cases. In 10 cases,
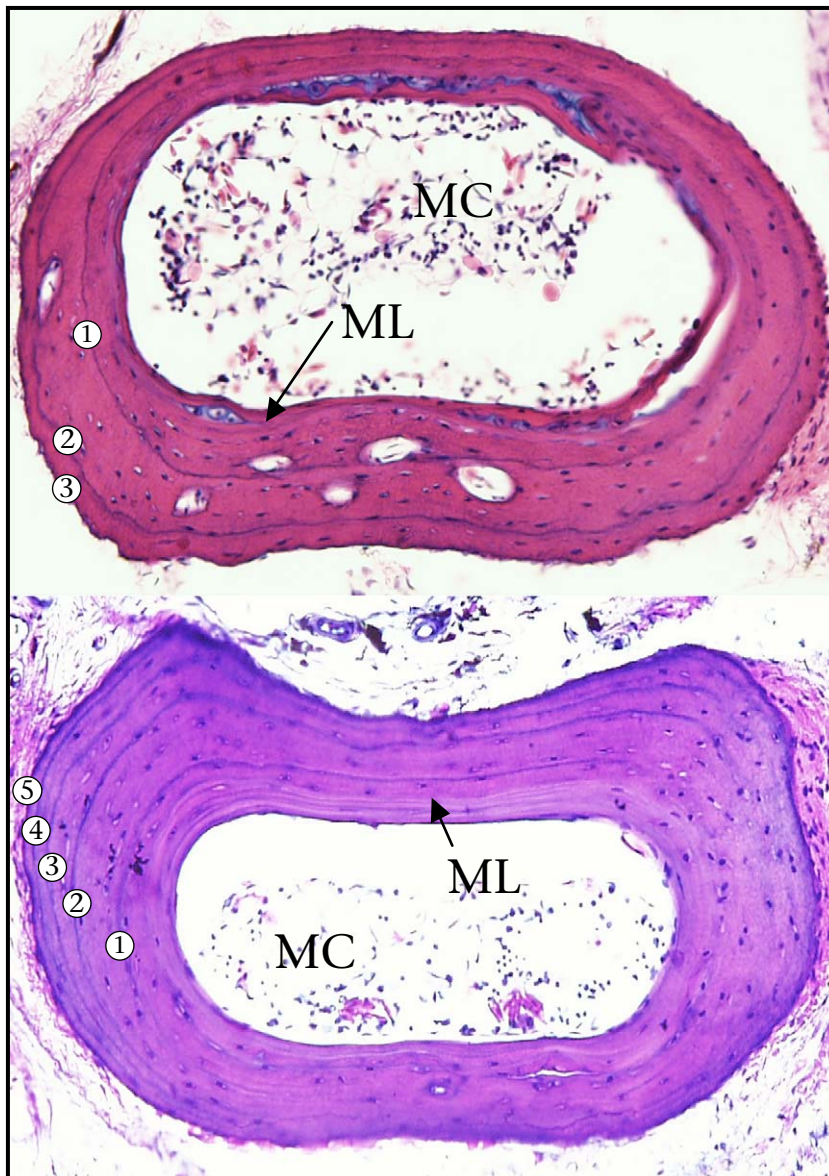

Figure 1. Phalangeal cross-sections of a 3-year-old *Bufo woodhousii* (top) and 5-year-old *B. cognatus* (bottom). MC represents the medullary cavity and ML represents the metamorphosis line.

estimates differed by 1 year and were reexamined to corroborate scores. Overall results were the same regardless of the age estimate used in the 10 cases where age estimates differed for the two observers.

For each individual, we measured the area (μm^2) of bone deposited between successive LAGs using Scion Image software (Scion Corp., Frederick, Maryland, U.S.A.). Area measures circumscribed by each successive LAG were made under constant magnification (40×) from digital images of a single histological section from the mid-diaphysis. Annual bone deposition (growth) was measured by calculating the area between successive LAGs or between the first LAG and the medullary cavity for year one (Fig. 1; see also Wake & Castanet 1995; Sullivan & Fernandez 1999; Measey 2001; Homan et al. 2003).

Statistical Analysis

We used ANOVA with behaviour as the class and snout–ischium length (SIL) as the dependent variable to test for size differences between calling and satellite individuals of *B. woodhousii* and *B. cognatus*. To determine whether age differed between calling and satellite individuals and whether age could be predicted by SIL in both species, we used ANCOVA with behaviour as the class, SIL as the covariate, and age as the dependent variable.

As a measure of size, we calculated the cumulative area of bone deposition at each age for each individual (except for one *B. cognatus* caller, for which the area could not be measured because of fragmentation of bone sections). The mean cumulative bone area at each age was calculated for callers and satellites for both *B. woodhousii* and *B. cognatus* and von Bertalanffy nonlinear regression curves were fit to the data to model growth and estimate growth rate. The von Bertalanffy growth equation is:

$$\text{Size} = A \times \left(1 - e^{-kt}\right)$$

where A is asymptotic size (cumulative bone area), e is the base of the natural logarithm, k is the characteristic growth rate, and t is age in years. Asymptotic size (A) for each species was determined by averaging the cumulative bone area of the five largest individuals (Frazer et al. 1990) and then k was calculated to estimate growth rate of callers and satellites. The von Bertalanffy growth model is the most commonly used and best-fit model in growth studies of ectothermic vertebrates (Andrews 1982; Busacker et al. 1990; Hota 1994). For both *B. woodhousii* and *B. cognatus*, we used a two-tailed *t* test (Zar 1999) to determine whether growth parameters (k values) significantly differed between callers and satellites. Lastly, we assessed the relationship between cumulative bone deposition and SIL in *B. woodhousii* and *B. cognatus* using linear regression. Regression analyses were done to corroborate that cumulative bone deposition is positively related to SIL and to equate differences in cumulative bone area between callers and satellites to differences in SIL for the two behavioural phenotypes. Data were analysed using SPSS v.10.0 (SPSS Inc., Chicago, Illinois, U.S.A.). Results were considered significant at $P \leq 0.05$.

RESULTS

Sampled male *B. woodhousii* ranged in age from 1 to 6 years, with SIL ranging from 63 to 91 mm. Male *B. cognatus* also ranged in age from 1 to 6 years, with SIL ranging from 70 to 98 mm. Males sampled while calling were significantly larger than males sampled while behaving as satellites for both *B. woodhousii* ($F_{1,51} = 5.97$, $P = 0.02$) and *B. cognatus* ($F_{1,24} = 4.82$, $P = 0.04$; Fig. 2). Body size differences between behavioural phenotypes have previously been reported for *B. woodhousii* and *B. cognatus* (Sullivan 1983; Krupa 1989; Leary et al. 2004). ANCOVA with age as the dependent variable, behaviour as the factor, and SIL as the covariate indicated no significant interaction between SIL and age for calling and satellite *B. woodhousii* ($F_{1,49} = 0.06$, $P = 0.80$) or calling and satellite *B. cognatus* ($F_{1,22} = 0.001$, $P = 0.99$), so the interaction term was removed from the models and ANCOVAs were run again. SIL was a poor predictor of age in both *B. woodhousii* ($F_{1,50} = 2.53$, $P = 0.12$) and *B. cognatus* ($F_{1,23} = 0.39$, $P = 0.54$). Males displaying the
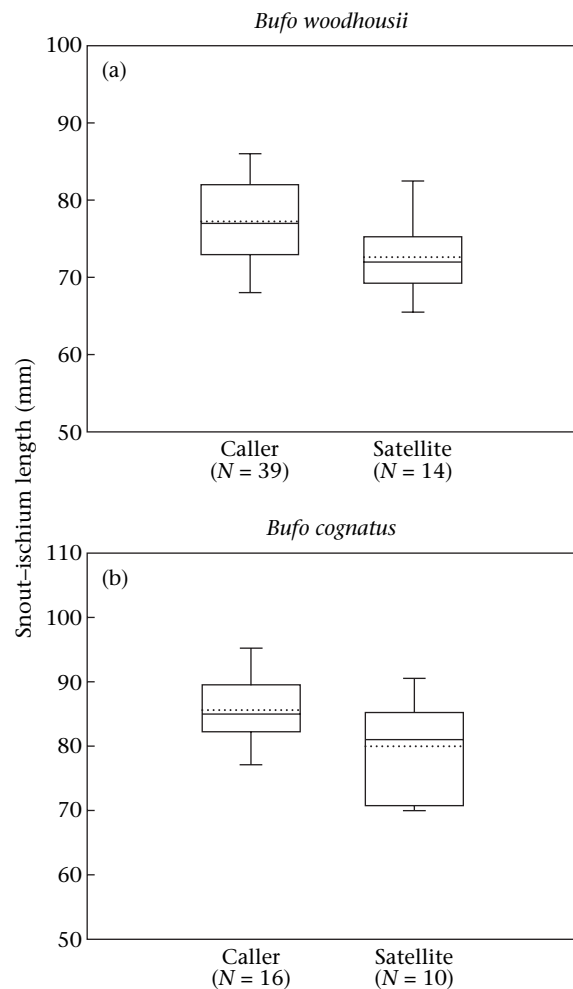

Figure 2. Box plots for snout–ischium length for male *Bufo woodhousii* (a) and *B. cognatus* (b) sampled as a caller or a satellite. Boxes represent 75th and 25th percentiles (interquartile range) and whiskers represent 90th and 10th percentiles. The dashed line is the mean and the solid line is the median.

two tactics did not differ in age for either *B. woodhousii* ($F_{1,50} = 0.001$, $P = 0.99$) or *B. cognatus* ($F_{1,23} = 0.36$, $P = 0.56$; Fig. 3).

Because individuals of both species that were sampled while adopting the satellite tactic were smaller, but not younger than individuals sampled while calling, our data suggest that individuals adopting satellite tactics had lower growth rates. Examination of bone deposition between successive LAGs indicated that growth rates were higher for males sampled as callers in both *B. woodhousii* (caller $k = 1.12$; satellite $k = 0.47$) and *B. cognatus* (caller $k = 0.44$; satellite $k = 0.37$; Fig. 4). The difference in growth rates between males sampled as callers or satellites was significant in *B. woodhousii* ($t_9 = 2.83$, $P = 0.02$), but not statistically different in *B. cognatus* ($t_9 = 0.51$, $P = 0.62$). Data were not available for all individuals at all ages. Hence, means for each age used in the growth models were based on different numbers of individuals. For example, all 15 *B. cognatus* callers provided growth data for ages 1, 2 and 3 years; 11 for age 4; three for age 5; and two for age 6. All 10 *B. cognatus* satellites provided growth data for age 1; nine for ages 2 and 3; four for age 4;

and three for age 5. All 39 *B. woodhousii* callers provided growth data for age 1; 20 for age 2; 16 for age 3; five for age 4; three for age 5, and one for age 6. All 14 *B. woodhousii* satellites provided growth data for age 1; seven for age 2; four for age 3; and one for ages 4 and 5.

Cumulative bone deposition was positively related to SIL in both *B. woodhousii* ($F_{1,51} = 52.02$, $P < 0.001$) and *B. cognatus* ($F_{1,23} = 12.88$, $P = 0.002$; Fig. 5). Based on these regressions, the 9402-μm^2 difference in bone area between caller and satellite *B. cognatus* at age 2 in the growth model equates to a 1.4-mm difference in SIL. The effect was more pronounced in *B. woodhousii*, where the 69 461-μm^2 difference in bone area at age 2 in the growth model equates to a 6.5-mm difference in SIL between callers and satellites.

Male *B. cognatus* sampled from Arizona and Oklahoma are potentially subject to different environmental conditions that could result in differences in age and/or growth for individuals from the two regions. However, we collected data from an equal number of satellites and callers from Arizona, and overall results were similar when individuals from the Arizona population were included or excluded from the analyses. In addition, Sullivan & Fernandez (1999) found no evidence to suggest that age
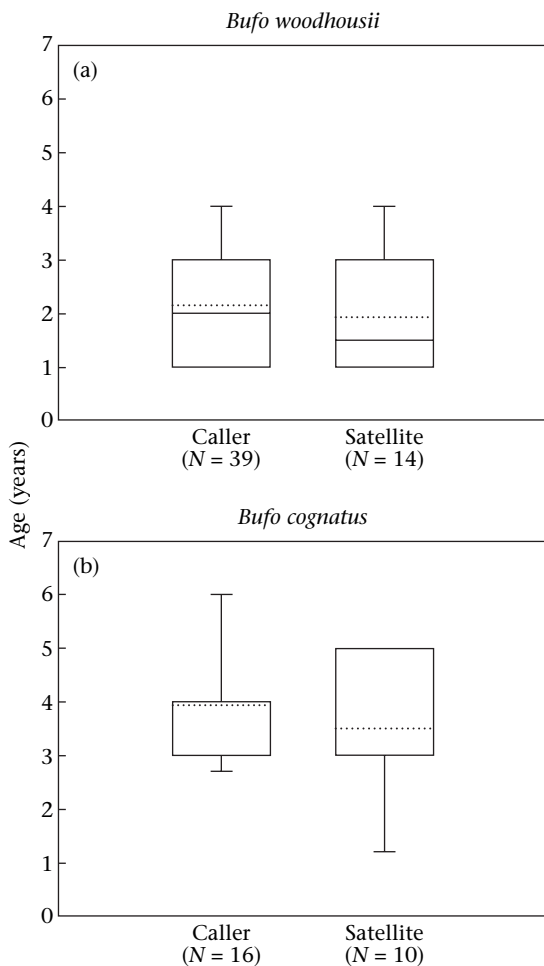

Figure 3. Box plots for age for *Bufo woodhousii* (a) and *B. cognatus* (b) sampled as a caller or a satellite. Boxes represent 75th and 25th percentiles (interquartile range) and whiskers represent 90th and 10th percentiles. The dashed line is the mean and the solid line is the median.
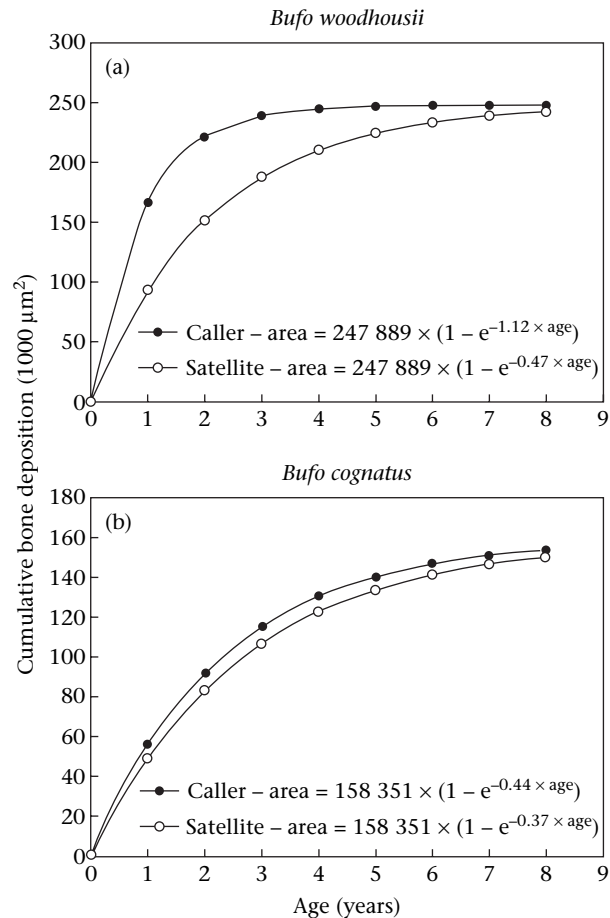

Figure 4. von Bertalanffy growth model curves for *Bufo woodhousii* (a) and *B. cognatus* (b) sampled as a caller or a satellite.

Bufo woodhousii

Bufo cognatus

$SIL = 0.000094 \times area + 61.4$
$R^2 = 0.51, P < 0.001$

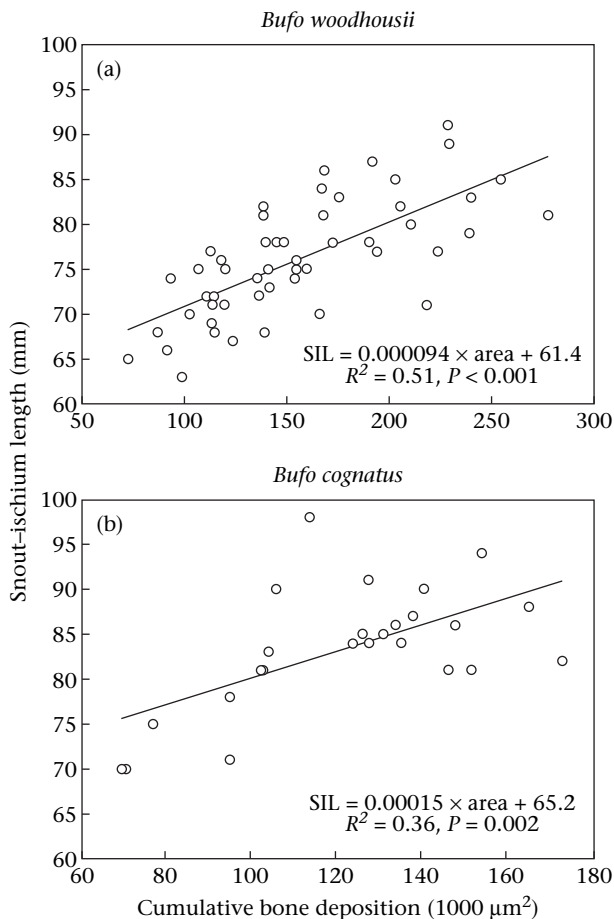$SIL = 0.00015 \times area + 65.2$
$R^2 = 0.36, P = 0.002$

Figure 5. Relationship between cumulative bone deposition and snout–ischium length for male *Bufo woodhousii* (a) and *B. cognatus* (b) sampled as a caller or a satellite.

structure of desert southwest anuran species (including *B. cognatus*) differs from those in more temperate regions. In fact, our age data for *B. cognatus* from Oklahoma are similar to their age data for *B. cognatus* from Arizona, further corroborating their conclusions.

DISCUSSION

Our results demonstrate that the expression of satellite tactics by the smallest male toads within a chorus in *B. woodhousii* and *B. cognatus* is not necessarily related to a male's age. These results are similar to those of Platz & Lathrop (1993), who indicated that size–age relationships are too variable to assume that satellite male chorus frogs (*Pseudacris triseriata*) are younger than larger calling males. However, Howard (1978, 1983, 1984) documented that smaller satellite bullfrogs, *Rana catesbeiana*, were younger than callers by using size-based age approximations ascertained by mark–recapture data. Eggert & Guyétant (2003) also suggested that alternative mating tactics were generally adopted by the smallest, youngest individual spadefoot toads, *Pelobates fuscus*, based on skeletochronologic analysis. Hence, size differences among individuals

adopting different mating tactics may reflect differences in age in some anuran species, but not in others.

Our results for *B. woodhousii* and *B. cognatus* are inconsistent with predicted relationships between age and the expression of alternative mating tactics. For instance, Howard (1978) proposed that one primary factor influencing satellite behaviour in iteroparous species should be a male's age, because younger males should differ considerably in size and/or experience that would affect the outcome of competition among conspecific males. However, the predicted age advantage does not hold for *B. woodhousii* or *B. cognatus* because size is a poor predictor of age (size has been shown to be a poor predictor of age for most anuran species examined, see Acker et al. 1986; Halliday & Verrell 1988; Kalb & Zug 1990; Jørgensen 1992). Secondly, the effects of prior experience may be of minimal impact on tactic expression in *B. cognatus* and *B. woodhousii* because, unlike *R. catesbeiana* and *P. fuscus*, these species are not territorial and do not engage in combat (Leary et al. 2004). Although males of both *B. cognatus* and *B. woodhousii* do frequently engage in physical encounters, these interactions consist primarily of short periods of amplexus among males. We view such interactions as mistakes in mate recognition rather than aggressive interactions (Leary 2001a, b). Hence, the predicted relationship between age and alternative mating tactics may only apply to species where age and size are tightly correlated and in species where smaller and younger males avoid aggressive interactions with other males.

Differences in size, but not age, for males that adopted calling versus satellite tactics in *B. woodhousii* and *B. cognatus* indicated that smaller individuals that were more likely to adopt the satellite tactic showed different growth rates than callers at some stage of development. Such a relationship was supported by differences in annual bone deposition for calling and satellite *B. woodhousii*. Although growth curves were not significantly different for calling and satellite *B. cognatus*, males of this species must also show different growth rates given that the behavioural phenotypes differed in size, but not age. Further analysis indicated that the differences in growth trajectories for callers and satellites potentially translate into 6.5-mm difference in SIL for *B. woodhousii* males of the same age and a 1.4-mm difference for *B. cognatus* males of the same age.

Differences in body size and growth trajectories among behavioural phenotypes suggest that not all male toads necessarily alternate between reproductive tactics. For instance, it is possible that only a subset of individuals within any given chorus adopt the alternative tactic when faced with conditions that potentially elicit satellite behaviour (i.e. low energy reserves). In populations of *B. woodhousii* and *B. cognatus*, these individuals appear to be the smallest males whose growth trajectories differ from those of callers. Similarly, both Sullivan (1983) and Krupa (1989) noted that some individual male *B. cognatus* do not appear to switch between tactics. We predict that this is also the case for males of many other anuran species given the commonly reported size discrepancy found between callers and satellites (reviewed by Halliday &

Tejedo 1995; Gerhardt & Huber 2002). For example, it is expected that if all individuals do, in fact, adopt a satellite tactic at some time, then there should be no body size difference between callers and satellites. However, body size differences among behavioural phenotypes have been found in several species even when analysed at several temporal scales (between nights of chorus activity, within nights of chorus activity, and across the entire breeding period, as well as across years).

We acknowledge the possibility that some males that we classified as callers in this study may have adopted satellite tactics at another time. Likewise, some individuals that were classified as satellites may have previously or subsequently adopted calling tactics. However, the crux of this investigation centres around the fact that individual satellites and callers that we sampled differed in body size, which is consistent with other studies (i.e. Sullivan 1983; Krupa 1989) and results found for numerous other anuran species (reviewed by Halliday & Tejedo 1995; Gerhardt & Huber 2002). However, despite differences in body size, there was no difference in age among these individuals. Hence, the common assumption that satellite males are maintained in a population through a subset of younger individuals adopting a satellite role is not supported.

Unfortunately, it is not possible, with the current data set, to determine whether differences in growth rates among males adopting caller versus satellite tactics are a consequence of the temporal frame in which offspring are produced. For instance, in the 4 years we studied these species in central Oklahoma, both species bred explosively (i.e. in 12 nights or less). In some years, however, intervals between periods of breeding activity may be separated by 2 months (C. J. Leary, unpublished data). Hence, offspring produced early in the season may attain greater size in the first year of development, which could result in more rapid growth trajectories compared to individuals produced later in the season.

Differences in morphology that are unrelated to differences in age among individuals practising alternative mating tactics may or may not be associated with genetic polymorphisms (West-Eberhard 2003), but often translate into differences in performance and fitness (Kingsolver & Huey 2003). For example, conditional satellite tactics could be associated with genetic differences among individuals if competitive ability has a genetic basis (Shuster & Wade 2003). Alternatively, conditional tactics may represent differences in behavioural responses among genetically monomorphic individuals (Gross 1986) that are constrained by environmental, morphological and/or physiological factors that affect performance (West-Eberhard 2003). In anurans, body size is the only reported morphological characteristic that typically differs among callers and satellites, but whether consistent genetic differences (i.e. polymorphisms) exist among males practising disparate mating tactics in any anuran species is still unknown. Stochastic variation in prey availability during development can impact growth rates and adult size (Madsen & Shine 2000) and could give rise to body size differences between callers and satellites.

Differences in developmental pathways frequently give rise to two or more morphological phenotypes that show disparate reproductive behaviours and, in some cases, developmental trajectories are impacted by food availability (reviewed by West-Eberhard 2003). For example, in male tree lizards, *Urosaurus ornatus*, individuals show different growth trajectories that correspond to alternative behavioural morphs (Thompson et al. 1993). In this species, circulating steroid hormone levels show a bimodal distribution in early ontogeny that suggests that the male morphs differ in the organizational effects of these hormones that then alter activational effects of the hormones in adulthood (Moore 1991; Moore et al. 1998). Endocrine regulation of alternative mating tactics in anuran amphibians may be related to the depletion of energy reserves during vocal production that then results in increased levels of circulating glucocorticoids, which then potentially affect sex steroid production (Mendonça et al. 1985; Marler & Ryan 1996; Burmeister et al. 2001; Emerson 2001) and/or neural activity involved in vocal production (Leary et al. 2004). In *B. woodhousii* and *B. cognatus*, high corticosterone levels were associated with the depletion of energy reserves (as measured by body mass) during calling activity (Leary et al. 2004). We have proposed that high corticosterone levels may alter the secretion of neuropeptides (i.e. arginine vasotocin, AVT) in vocal control centres of the brain that mediate vocal behaviour (Leary et al. 2004; see Marler et al. 1999 for AVT-immunoreactivity differences in calling and satellite cricket frogs, *Acris crepitans*). Whether different developmental trajectories subject the smallest adults to more rapid rates of energy depletion that drive corticosteroid-mediated behavioural responses or whether alternative behavioural phenotypes experience organizational effects during development that alter activational effects of hormones and behavioural expression in adulthood have not been examined in any anuran species. We are currently pursuing this question in these two toad species.

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